

Review

Florian Weinberger*, Tiina Paalme and Sofia A. Wikström

Seaweed resources of the Baltic Sea, Kattegat and German and Danish North Sea coasts

<https://doi.org/10.1515/bot-2019-0019>

Received 30 March, 2019; accepted 8 October, 2019; online first 12 November, 2019

Abstract: Due to low salinity and lack of hard substrata, the Baltic Sea and Kattegat area and German and Danish North Sea coasts are characterized by a relatively low diversity of seaweeds. At the same time the areas are severely eutrophicated, which has caused extensive shifts in macroalgal communities toward opportunistic species. Unattached seaweed communities dominated by *Furcellaria lumbricalis*, which have been a resource for hydrocolloid production since the 1940s, have been severely reduced due to eutrophication and unsustainable harvesting and are nowadays only exploited commercially in Estonia. On the other hand, the biomass of opportunistic seaweeds of various red, green and brown algal genera has increased. They cause ecological problems, are a nuisance on many tourist beaches and constitute at the same time a potential bioresource that is so far only exploited to a limited extent for production of energy and fertilizer. Commercial seaweed cultivation is largely focused on *Saccharina latissima* and still very limited, but is currently being expanded as a compensation measure for sea-based fish aquaculture. Also land-based seaweed cultivation is primarily employed for recycling of nutrients in tank animal aquaculture, but in most cases so far only on an experimental scale.

Keywords: eutrophication mitigation; *Furcellaria lumbricalis*; *Saccharina latissima*; seaweed aquaculture; seaweed harvesting.

Introduction

This publication provides an update to an earlier article by Schramm (1998), who already gave a detailed description of the macroalgal species distribution and diversity along SE North Sea and Baltic Sea coasts. During the last two decades several species introductions into the region have been recorded [for example, approximately 10 on German coasts (Lackschewitz et al. 2014, Steinhagen et al. 2018)] and also range shifts of species were observed within the area (Kovtun et al. 2009, Steinhagen et al. 2018). Nonetheless, the general distribution patterns outlined by Schramm (1998) still remain valid. At the German and Danish West coasts, natural hard substratum that would allow for algal settlement is extremely rare and is almost only available around the German island of Helgoland, where 322 species of macroalgae have been recorded at least once up to 2009 in a limited area of approximately 50 km² (Bartsch and Kuhlenskamp 2000, Schories et al. 2009a,b; see Figure 1). This diversity contrasts with only 113 and 112 species that have been found in the North Friesian and East Friesian Wadden Seas, respectively (Schories et al. 2009a,b), areas that are much larger than the rock shelf around Helgoland, but characterized by extended mud and sand flats and high water turbidity. Scarcity of hard substrata together with particularly low macroalgal diversity also characterizes the Baltic Sea coasts of Poland and Latvia, while most other Baltic Sea coasts offer more favorable substrata. Bedrock occurs along Swedish, Finnish and Estonian coasts and on the Danish island of Bornholm, and smaller hard substrata such as pebbles, stones or boulders are frequently encountered mingled with soft bottoms in the remaining areas. However, large parts of the Baltic Sea are characterized by low salinities that limit its suitability as a habitat for seaweeds and marine organisms in general. The mean surface salinity decreases from fully marine conditions at the northern tip of Denmark to 8 at the entrance to the inner Baltic Sea (Darss Sill) and 7 in the central Baltic Sea (Gotland basin; Figure 1), and this correlates with a decrease in macroalgal diversity by approximately 50% and 75%, respectively

*Corresponding author: Florian Weinberger, GEOMAR Helmholtz-Institute for Ocean Science, Marine Ecology Division, D-24105 Kiel, Germany, e-mail: fweinberger@geomar.de. <https://orcid.org/0000-0003-3366-6880>

Tiina Paalme: Estonian Marine Institute, University of Tartu, Tartu, Estonia

Sofia A. Wikström: Baltic Sea Centre, Stockholm University, SE-106 91 Stockholm, Sweden



Figure 1: Types of coastlines, annual average sea surface salinities, and species numbers of algal macrophytes that have been recorded in different sea areas of the Baltic Sea and the German and Danish North Sea.

Modified from Rönnbäck et al. (2007); species numbers are from HELCOM (2012) for the Baltic Sea and from Schories et al. (2009a,b) for the North Sea.

(Figure 1). As predicted by Remane (1934) – who argued that taxonomic diversity of macrobenthic organisms should be generally lowest within the horohalinicum (salinities of 5–8) – the areas with even lower salinity (the Bothnian Sea and Gulf of Finland) have a slightly higher diversity due to increased presence of freshwater species (but see Schubert et al. 2011). Ice scraping in winter causes unfavorable conditions and again lower diversity in the northern Baltic (Kovtun et al. 2009).

Coastal areas of the south-eastern North Sea and large parts of the Baltic Sea, including the Kattegat, have been heavily eutrophicated for decades (Almroth and Skogen 2010, Gustafsson et al. 2012). This has caused substantial compositional shifts in the macroalgal communities, with a general decline in large, perennial species, and an increase in opportunistic species (Schramm 1996, 1998). Since the 1980s, the nutrient load to the Baltic Sea and North Sea has decreased strongly due to improved wastewater treatment and other measures to reduce nutrient emissions from land (Gustafsson et al. 2012). The shift back to a less eutrophic ecosystem state is however slow (Gustafsson et al. 2012, Riemann et al. 2015). Clear signs of recovery of perennial seaweed species are seen in some coastal areas, such as central Sweden or Estonia (Eriksson et al. 1998, Torn et al. 2006, EEA 2018), but not in others, such as Germany or Poland, where surface runoff still discharges excessive amounts of waste nutrients from agriculture into coastal waters (Rohde et al. 2008, Schories et al. 2009a,b, EEA 2018).

The Baltic Sea salinity gradient is not only a reason for decreased algal diversity but, for many species, also a

reason for decreased growth rate and dwarfed morphologies (Russell 1988). Together, these possibly explain the relatively weak tradition of exploiting and using natural seaweed resources in the area – apart from occasional application of beachcast seaweed as fertilizer by local farmers – until the exploitation of *Furcellaria* for phycolloid production started in the early 1940s (Schramm 1998). Since the 1980s, an increasing number of pilot studies have attempted to utilize the seaweed resources in the region, through harvesting of natural biomass as well as sea-based and land-based aquaculture. In the following sections we will mainly focus on activities related with harvesting of *Furcellaria lumbricalis*, with cultivation of *Saccharina latissima*, and with harvesting of beach cast algal biomass.

Harvest of *Furcellaria lumbricalis*

As already recognized by Lehmann (1814) the pristine Baltic Sea environment is characterized by the presence of relatively large amounts of unattached and drifting perennial seaweeds and seagrasses that provide a potential bioresource. In deeper water this resource is often composed of *Furcellaria lumbricalis*, which up to the present has remained the only seaweed species in the Baltic Sea that is harvested on a commercial scale. *Furcellaria lumbricalis* has attached and unattached (loose-lying) thallus forms, which represent two distinctive ecotypes (Kersen 2013). The attached *F. lumbricalis* is widely distributed on hard substrata in the Baltic Sea and can be found at

salinities down to 3.6 (Snoeijs 1999, Kostamo 2008, Bučas et al. 2009, Kersen et al. 2009, Kostamo et al. 2012). The unattached form of the species has a long harvesting history in the Baltic Sea. Its industrial exploitation started in the mid 1940s and lasted until the mid 1960s in Danish waters in the central part of the Kattegat (Schramm 1998). Nowadays unattached *F. lumbricalis* in the Baltic Sea inhabits only semi-exposed habitats with soft bottoms of the West Estonian Archipelago Sea area (Martin et al. 2013), but outside the Baltic it can also be found in the lochs of Scottish and Irish seas (Levring et al. 1969). The communities of unattached *F. lumbricalis* previously found in Polish waters (Schramm 1998) disappeared due to elevated eutrophication in the 1980s (Kruk-Dowgiałło and Szaniawska 2008), while intensive harvesting decimated the drifting *Furcellaria* stocks in the central Kattegat in the

1950s–1970s (Lund and Christensen 1969, Schramm 1998, Pedersen and Snoeijs 2001).

The Kassari Bay, the western basin of the West Estonian Archipelago Sea still hosts a loose-lying red algal community dominated by unattached forms of *Furcellaria lumbricalis* and *Coccotylus truncatus* (Figure 2). The community inhabits sandy and sandy clay substrata, where it forms up to 30-cm thick carpets on seabed at depths of 5–9 m (Martin et al. 2006b). The mixed community of loose-lying *F. lumbricalis* and *C. truncatus* in Estonia was first described in the early 1960s, and at that time the total biomass was estimated to be 150,000 t wet weight (ww; Kireeva 1961, 1965). More detailed descriptions and assessments of the structure of the community were given by Trei (1978), who estimated the total community biomass to be 140,000 t ww, covering an area of 140 km². During the 1980s and 1990s a remarkably lower total biomass and smaller distribution area of the red algal community was observed, which was due to overgrowth by the opportunistic filamentous brown alga *Pylaiella littoralis* (Martin et al. 1996). This was followed by a recovery of both the total biomass and the total area of the community, and since 2011 *F. lumbricalis* stocks in Estonia have remained stable (Figure 3).

In 2017 the total community biomass was estimated to be 179,000 t ww. It covered an area of 170 km², with a mean coverage of 78% and a mean thickness of the algal mat of 6 cm (Paalme 2017). On average, *Furcellaria lumbricalis* accounts for 60–73% (612–1010 g m⁻²) and *Coccotylus truncatus* for 13–25% (147–309 g m⁻²) of the total community biomass (Figure 4). Among nine macroalgal species that are associated with the dominating species in the community, the red algae *Ceramium tenuicorne* and *Vertebrata fucoides*, the brown alga *Battersia arctica* and the green alga *Chaetomorpha linum* were most common (Pärt 2013).

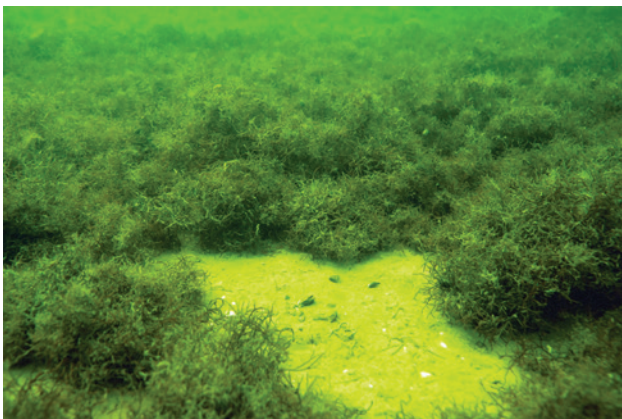


Figure 2: Loose-lying *Furcellaria lumbricalis*-*Coccotylus truncatus* community in the Kassari Bay, West Estonian Archipelago Sea (Photo: K. Kaljurand).

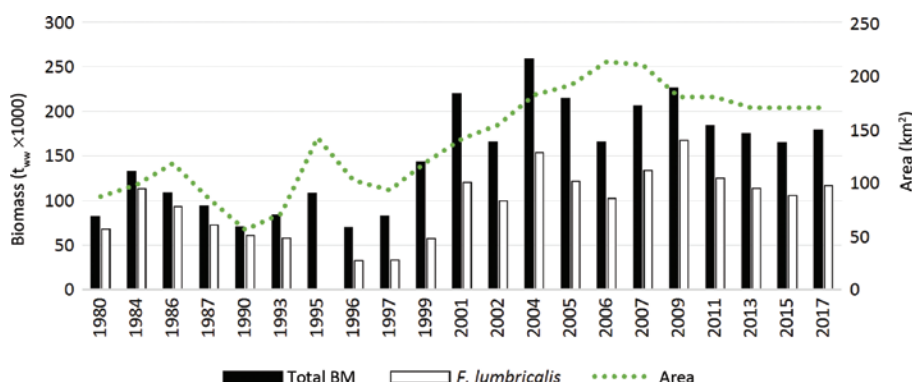


Figure 3: Interannual variation (1980–2017) of the total community biomass (BM), the total *Furcellaria lumbricalis* biomass and the area of the loose-lying red algal community in the Kassari Bay, West Estonian Archipelago Sea.

Data after Martin et al. (2006a), updated with data of the Estonian Marine Institute on annual monitorings 2003–2017.

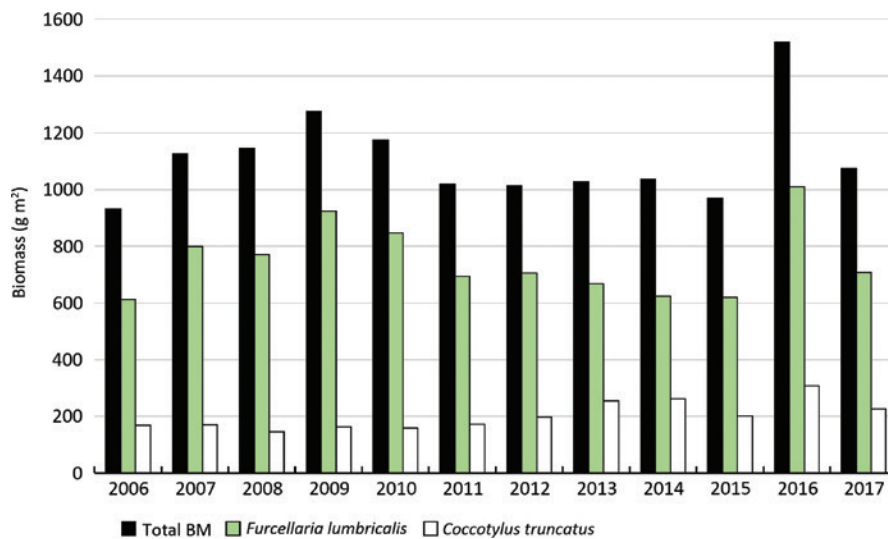


Figure 4: Interannual variation (2006–2017) of the share of *Furcellaria lumbricalis* and *Coccotylus truncatus* in the loose-lying red algal community biomass (BM) in the Kassari Bay, West Estonian Archipelago Sea. Compiled results of annual monitorings 2006–2017; database of the Estonian Marine Institute.

Unattached *Furcellaria lumbricalis* is characterized by relatively slow growth. Its growth rate is primarily affected by factors that alter the light availability for photosynthesis, i.e. seasonality, water transparency, depth and density of the algal community (Martin et al. 2006a,b, Kotta et al. 2008, Paalme et al. 2011, 2013). The commercial utilization of the loose-lying *F. lumbricalis* and *Coccotylus truncatus* community in Kassari Bay was started in 1966 by the local company ESTAGAR (ESTAGAR 2019) and until now it has been mostly based on the extraction of furcellaran, that is widely used as a stabilizing, thickening and gelling agent in the food, pharmaceutical, cosmetics and agriculture industries (Tuvikene et al. 2006, 2010, Tuvikene and Robal 2015a, Kersen et al. 2017). Furcellarans of *F. lumbricalis* from the Baltic Sea are characterized by unique chemical composition and properties, as they are a hybrid of κ and β carrageenan (Tuvikene et al. 2006, Tuvikene and Robal 2015a). At present, there is an increasing interest in a new potential biotechnological application of unattached *F. lumbricalis* biomass as a raw material for extraction of the red pigment R-phycoerythrin (Tuvikene and Robal 2015b, Kersen et al. 2017). Due to its different bioactive properties, R-phycoerythrin can be used not only in the food industry as a natural food colorant, but also in medicine and cosmetics (Kersen et al. 2017).

To assure environmentally sustainable and long-lasting utilization of the unique loose-lying red algal community, its ecological status has been monitored regularly, and official regulations of harvesting were introduced since the start of its commercial exploitation (Martin et al.

1996). Currently harvesting by bottom trawling is limited to 2000 t ww per year (Paalme 2017). In addition, beach deposits of both loose-lying and attached communities of *Furcellaria lumbricalis* are collected for commercial utilization of carrageenans. Annual losses of the loose-lying *F. lumbricalis*-*Coccotylus truncatus* community through wrack deposits were estimated at about 4800 t ww per year, i.e. 4% of the community standing stock (Kersen and Martin 2007, Kersen 2013).

Beach wrack as a potential bioresource

Beach wrack deposition is not a new phenomenon in the Baltic Sea but, as outlined below, the shift in macrophyte communities toward more opportunistic macroalgal species since the onset of eutrophication (e.g. Schramm 1996, 1998, Ronnberg and Bonsdorff 2004) has resulted in a change in composition and amount of beach wrack. There are few historical records of the composition and amount of beach cast macrophytes and seaweed drifting in shallow waters of the Baltic Sea, but 200 years ago in the vicinity of Copenhagen Lehmann (1814) observed “overwhelmingly *Zostera marina*, but also algae”. In contrast, *Fucus* contributed 75% to the dry weight (dw) of biomass that was analyzed in August 1977 on 20 plots along the Baltic Sea coast of the German state of Schleswig-Holstein, and the remaining part was composed of other

algae and eelgrass (Grave and Moeller 1982). Repetitions of this study in 2012 and 2013 on the same coastal section and based on the same methodology (Weinberger et al. 2013) found significantly less *Fucus* (21 and 17%, respectively) and more eelgrass (37 and 49%) and other algae (42 and 34%), which were mostly opportunistic species that belonged to the genera *Ceramium*, *Vertebrata*, *Cladophora*, *Pylaiella* and *Ulva* (for some typical views see Figure 5). A strong dominance of opportunists in drifting and beach cast seaweed was also observed during the last two decades on many other Baltic Sea coasts, for example in Poland (Filipkowska et al. 2009, Bucholc et al. 2014), South Sweden (Bucholc et al. 2014, Risén 2014), South-east Sweden (Malm et al. 2004), Estonia (Paalme et al. 2004), South West Finland (Vahteri et al. 2000) and the Åland archipelago (Berglund et al. 2003).

Quantitative historical data of beach wrack abundances exist for Northern Germany (Grave and Moeller 1982), which allowed for a direct comparison of former and recent amounts (Weinberger et al. 2013). In August 1977, algae washed up along the shoreline of Schleswig-Holstein had a mean dw of 1 kg m^{-2} (Grave and Moeller 1982),

while 3.5 kg m^{-2} and 2.6 kg m^{-2} were present in August 2012 and August 2013, respectively (Weinberger et al. 2013). At the same time the area covered by beached seaweed – in both cases quantified by black and white aerial photography on the same coastal section of 360 km – increased from $900 \text{ m}^2 \text{ km}^{-1}$ beach line in August 1977 (Grave and Moeller 1982) to $1150 \text{ m}^2 \text{ km}^{-1}$ beach line in August 2012 (Weinberger et al. 2013). Together these data suggest that the quantities of beached biomass in Schleswig-Holstein increased from 0.9 t dw km^{-1} coast line in 1977 to 4.0 t dw km^{-1} coast line in 2012. At the same time the total amount of beached *Fucus* remained approximately stable, while that of other, mainly opportunistic seaweeds increased by a factor of at least 7.5 (Weinberger et al. 2013).

In order to estimate the rate of beach wrack deposition, Mossbauer et al. (2012) analyzed series of images generated by beach cameras in 11 municipalities in Germany between May and October 2010. By quantifying beach areas covered with seaweed in time intervals of 3 h and using the biomass density value of 1 kg m^{-2} given for 1977 (Grave and Moeller 1982) the authors found a total amount of 6.8 t dw km^{-1} of beach wrack that accumulated within a

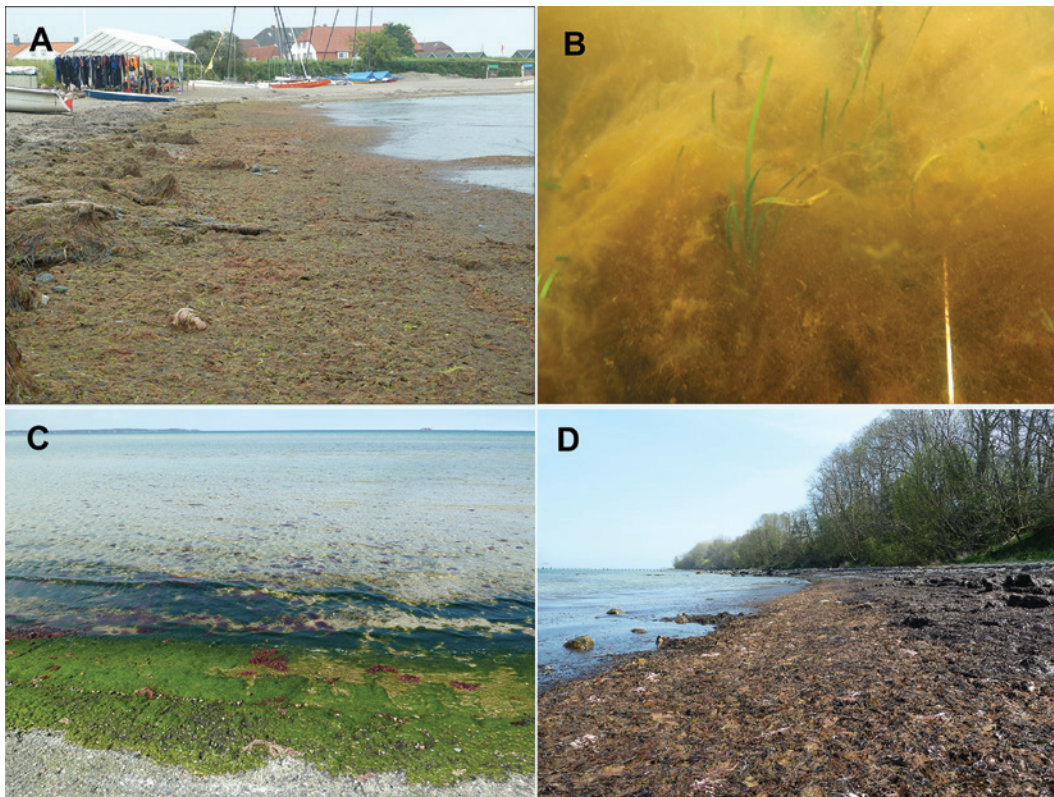


Figure 5: Different views of macroalgal blooms on German Baltic Sea coasts.

(A) Beach wrack dominated by *Ceramium virgatum*, Hohwacht, 16.8.2012 (Photo © F. Weinberger). (B) Mat of *Pylaiella littoralis* covering a meadow of eelgrass, Mönckeberg, 15.5.2013 (Photo © C. Lieberum). (C) Beach wrack dominated by *Cladophora* sp., Stein, 12.4.2014 (Photo © M. Hammann). (D) Beach wrack composed of various red algae and eelgrass, Neukirchen, 30.4.2012 (Photo © F. Weinberger).

period of 168 day. However, as the density of beach wrack in the area is today approximately 3 times higher than 1977 (see above) a value of 20 t km^{-1} might be more realistic, which could mean that at least 45,000 t dw of biomass are washed ashore along the German Baltic Sea coast each year.

According to other coarse estimates, altogether around 60,000 t dw of seaweeds may accumulate on beaches in southern Sweden each year (Blidberg and Gröndahl 2012). We have not found comparable estimates for other countries, but high accumulation has been documented in parts of the Estonian, Lithuanian and Polish coasts (Blidberg and Gröndahl 2012, Bucholc et al. 2014). Very large amounts of biomass were found on the island of Öland in SE Sweden: During monthly measurements from 1999 to 2001 (Malm et al. 2004) found particularly high amounts in September that ranged from 4000 to $12,000 \text{ m}^3 \text{ km}^{-1}$ coastline. Following Bergström (2012) these quantities would correspond to 700–2100 t of total solids km^{-1} .

Small-scale collection of beach wrack occurs in several parts of the Baltic Sea region. For example, in 23 seaside resorts along the German Baltic Sea coast, in the Polish community of Sopot and in the Swedish community of Trelleborg between 26.9 and 135 t of wet biomass are on average removed per year and km of beach line together with variable amounts of sand (Davidsson 2007, Gröndahl 2009, Mossbauer et al. 2012, Bucholc et al. 2014). The harvested beach wrack composition varies among areas, but also among seasons, depending on the dynamics of the local seaweed populations (Weinberger et al. 2013). In most cases, the primary motivation to collect beach wrack is to get rid of the seaweeds from sandy shores, where visitors and authorities perceive them as harmful or disgusting (Filipkowska et al. 2009, Mossbauer et al. 2012). The collected seaweed is therefore seen as a waste product and a considerable part is dumped and sometimes tipped back into the sea after the bathing season (Mossbauer et al. 2012, Risén et al. 2017). However, some of the collected seaweed is used as biofertilizer in agriculture or gardening (Mossbauer et al. 2012, Michalak et al. 2016, Franzén et al. 2019). Beach cast seaweed was traditionally used as fertilizer and soil conditioner in the Baltic Sea region (Greger et al. 2007, Franzén et al. 2019), but the use decreased when mineral fertilizers were introduced in the 1950s (Franzén et al. 2019). In view of the current problems with large-scale eutrophication of the Baltic Sea and the increasing awareness that mineral phosphorus is a limited resource, there is a renewed interest in reviving this practice in order to capture nutrients from the sea and use it for crop production (Blidberg and Gröndahl 2012, Franzén et al. 2019).

A challenge for using Baltic Sea seaweed as biofertilizer is that it sometimes contains high concentrations of heavy metals such as cadmium, which the crop takes up (Greger et al. 2007). Seaweeds are known to accumulate heavy metals from seawater and accumulation may be increased in the low salinity of the Baltic Sea since it increases bioavailability of metals (Steinhagen-Schneider 1981). Because of the high cadmium content, Greger et al. (2007) suggested that seaweeds from the Baltic Sea should only be used in cultivation of non-edible crops. However, the reported heavy metal content in Baltic Sea seaweed varies widely and a number of studies show relatively low cadmium content (reviewed by Bergström 2012; see also Michalak et al. 2016, Suutari et al. 2017, Franzén et al. 2019). This suggests that Baltic seaweeds may be a safe biofertilizer also for edible crops, but more research is needed on how the heavy metal content in beach cast seaweed varies among regions, seasons and seaweed species.

Another potential use for drifting and beach cast seaweed is biofuel production. Utilization of seaweed biomass to produce renewable energy has been discussed since the 1970s, but is still under technical development (e.g. Suutari et al. 2017). A number of pilot projects in the Baltic Sea area have tested methods to produce biogas from beach cast. For instance, the Swedish municipality Trelleborg tested biogas production through anaerobic digestion in a customized biogas plant, using the residue as biofertilizer in agriculture (Risén et al. 2014). The results show that it is possible to achieve a positive energy balance for the biogas production (Risén et al. 2014), but also that there are considerable practical challenges including handling of the sand mixed in with the seaweed and the high salt, sulfur and sometimes cadmium levels in the biomass that limit its usefulness as fertilizer. The Danish municipality Solrød recently constructed a biogas plant that was specifically designed for anaerobic degradation of beach cast seaweed mixed with manure and carrageenan and pectin production waste. The facility was designed for treatment of $200,000 \text{ t}$ of biomass yr^{-1} and predicted to give a biogas production of $40,000 \text{ t CO}_2$ equivalents per year (Kaspersen et al. 2016).

While the pilot projects have concluded that biofuel and fertiliser production from beach wrack and the mentioned seaweeds is feasible, the cost for this small-scale, customized production is presently too high to be competitive. Still, some actors see it as an attractive environmental management strategy since it can have a number of societal benefits (Blidberg and Gröndahl 2012). For instance, harvest of beach wrack leads to removal of nutrients contained in the biomass, which would otherwise

leak back to the Baltic Sea environment during decay. Due to the large negative consequences of eutrophication in the Baltic Sea, reducing nutrient loads to the sea is a top priority in the catchment area, as demanded by the EU water framework directive (European Parliament and Council 2014). Harvest of beach wrack will have a minor effect on the large-scale eutrophication, even with optimistic estimates of harvest potential (Bucholtz et al. 2014) but, in areas where large amounts are harvested, it may decrease the local nutrient load substantially (Kaspersen et al. 2016). Consequently, a study of non-market values of beach cast management indicated that local residents in southern Sweden have a high willingness to pay for an environmental program that removes seaweeds from beaches and uses the biomass for production of biogas (Risén et al. 2017).

However, when motivating beach wrack collection with positive environmental effects, it is important to acknowledge that harvesting of seaweed is *per se* a disturbance of the coastal environment. Frequent grooming of beaches to collect seaweed litter reduces the species richness and ecological diversity of sandy coasts and increases the risk of beach erosion (Malm et al. 2004, Defeo et al. 2009, Vanhooren et al. 2011, Gilburn 2012), which is a recurring problem on North Sea coasts (Vollbrecht 1973) and elsewhere (Haller et al. 2011) in the area. Similarly, collection of drifting seaweed or algal mats from shallow water would not be without disturbing impact. The net environmental effect of harvesting drifting seaweeds probably depends on their density and could be either positive or negative. Drifting algae can provide ecological services to the coastal environment (Salovius et al. 2005, Nyberg et al. 2009). On the other hand, dense blooms or mats of unattached opportunistic seaweeds that typically develop as a result of eutrophication, such as *Ceramium tenuicorne*, *Vertebrata fucoides*, *Chaetomorpha linum*, *Cladophora* species or *Ulva* species (Norkko and Bonsdorff 1996a,b, Schramm 1998, Hammann et al. 2013, Steinhagen et al. 2018), also have negative impact on the Baltic Sea and Wadden Sea environment. They very often cause anoxia and environmental deterioration (Norkko and Bonsdorff 1996a,b, Osterling and Pihl 2001, Lauringson and Kotta 2006, Holmer and Nielsen 2007, Arroyo et al. 2012, Hammann et al. 2013, Quillien et al. 2016, Steinhagen et al. 2018) and in the short term their removal could be a countermeasure against these negative effects. Integrated assessments of the market values, non-market values and damage that may be generated by harvesting of opportunistic seaweeds from shallow waters are still largely missing (Blidberg and Gröndahl 2012). Given the large variability of eutrophication status,

possible harvesting techniques and other environmental parameters in the region, such assessments could potentially result in different conclusions for different coastal regions.

Seaweed aquaculture

Commercial sea-based aquaculture of seaweeds in the region is currently restricted to Denmark and Germany. As along other cold temperate coasts of Europe the main target species is the kelp *Saccharina latissima*, which is generally capable of relatively fast growth. However, the species reaches its distribution limit in the Baltic Sea salinity gradient at Bornholm (Møller Nielsen et al. 2016) and is currently only cultivated at locations with annual mean sea surface salinities of at least 16 (Kiel Fjord, Germany; Sandow 2007), which already cause significantly reduced growth (Bartsch et al. 2008). In 2015 commercial sea-based farming of *S. latissima* was carried out in seven licensed areas in Denmark (Ferdouse et al. 2018) and in one area in Germany (Wang et al. 2019). The largest of these farms had a size of 1 km² and the production volume in Denmark increased from 1 t in 2009 to 10 t (ww) in 2014 (Ferdouse et al. 2018).

While commercial seaweed farming is still restricted, a number of pilot projects have been launched to develop seaweed farming in the area. In Sweden the efforts are mainly concentrated in the west coast, where the salinity is >20. The “Seafarm project” – involving five Swedish universities – was launched in 2014 to foster research around a cultivated *Saccharina latissima* biorefinery supply-chain, which resulted in the establishment of a first experimental seaweed farm in the Koster archipelago in Skagerrak (Hasselstrom et al. 2018). A number of studies conducted in Denmark also estimated the regional potential of cultivated kelps or *Ulva lactuca* for production of biogas, bioethanol, biobutanol and more advanced biorefineries (Bruhn et al. 2011, Alvarado-Morales et al. 2013, Hou et al. 2015). The low salinity in the inner parts of the Baltic Sea is still seen as a major limitation to seaweed farming (Blidberg and Gröndahl 2012). However, in Estonia several pilot projects funded by the Estonian Environmental Investment Centre and the European Maritime and Fisheries Fund have been initiated to develop cultivation techniques for both unattached and attached forms of *Furcellaria lumbricalis* and to estimate the environmental impact of different cultivation methods.

In the SE North Sea, seaweed aquaculture is primarily limited by lack of sheltered sites. For this reason one of the first techniques for offshore cultivation of *Saccharina*

latissima has been developed since the early 1990s in this area, patented and described in detail elsewhere (Buck and Buchholz 2004, Bartsch et al. 2008, Buck and Grote 2019). The system is now discussed for co-use with offshore structures such as wind farms (Buck and Grote 2019), that are currently under construction in the German Bight and elsewhere. However, infrastructures exposed to high-energy environments generally require more extensive capital investment and pose larger risks of losses than infrastructures in sheltered sites (Buck and Grote 2019), which reduces the potential margins for profits.

The primary target products of seaweed aquaculture in the Baltic and SE North Sea region were so far food (Lüning and Mortensen 2015) and ingredients for cosmetics (Sandow 2007), but the potential for production of more specific ingredients that can generate added value, such as pharmaceuticals or food additives, is also increasingly explored (Marinho et al. 2015b, Veide Vilg et al. 2015, Bruhn et al. 2016, Nielsen et al. 2016). In addition, exploitation of the bio-mitigation capacity of cultivated seaweed in the framework of integrated multitrophic aquaculture (IMTA), or as a compensation for increased animal aquaculture is coming more and more into focus (e.g. Sandow 2007, Holdt and Edwards 2014, Marinho et al. 2015a, Bruhn et al. 2016, Hasselstrom et al. 2018, Buck and Grote 2019). For example, seaweed cultivation is explicitly mentioned in Denmark's National Strategic Plan for the Development of Sustainable Aquaculture 2014–2020 as a compensation measure to bioremediate waste nutrients of fish and shellfish aquaculture (Ministeriet for Fødevarer Landbrug og Fiskeri 2016) and the Danish Government is currently seeking to facilitate investment in the creation of zones with integrated aquaculture (Ferdouse et al. 2018). The goal is to prevent a deterioration of water quality in the Danish marine areas despite a predicted increase in fish aquaculture by at least 25% by 2020. Also in Sweden, the ecosystem services that can be provided by seaweed farming are increasingly recognized as relevant benefits (Pechsiri et al. 2016, Hasselstrom et al. 2018).

In contrast to sea-based aquaculture, land-based aquaculture is *per se* fully or largely independent of marine environmental conditions, which gives the opportunity to manipulate to a certain extent the biochemical composition of the produced seaweed (Hafting et al. 2012). Since 2006 a commercial land-based seaweed farm on the German North Sea island of Sylt has produced *Saccharina latissima* in outdoor tanks for food. However, after some years the production line was moved to Norway (Bundesverband Aquakultur 2019). Land-based production of seaweed has been and is still tested on pilot scale in several countries in the region. The target species are

diverse, including *Fucus vesiculosus*, *Furcellaria lumbri-calis* (Haglund and Pedersén 1988), *Ulva intestinalis* (F. Gröndal, pers. comm) and *Ulva fenestrata* (S. Steinhagen, pers. comm.) but also exotic species, such as *Agarophyton tenuistipitatum* (Haglund and Pedersen 1993), and the goal is often less the direct production of seaweed than nutrient recycling in land-based aquaculture of fish (Haglund and Pedersen 1993). Many of these research activities involve small and medium sized players from the private sector and detailed information is scarce.

Toward the future

In conclusion, the suboptimal geographic conditions constitute an important limitation to the production of seaweed and seaweed-based products in both the Baltic Sea and the SE North Sea. Nonetheless, farming of *Saccharina latissima* has been initiated in areas with salinities of at least 16 in the Western Baltic Sea, the Kattegat and the North Sea. In the low salinity of the Baltic Sea proper, industrial harvesting of unattached *Furcellaria lumbri-calis* is now restricted to Estonia, due to depletion of this seaweed stock in other coastal areas. Current research aims to identify new applications for these and other seaweed species that are present in the area. While the suboptimal conditions limit the profitability of the industry to some extent, seaweed harvesting and seaweed aquaculture are currently promoted as a way to decrease the nutrient load to eutrophic coastal areas and to mitigate the negative symptoms of eutrophication (Seghetta et al. 2016). Seaweeds also gain in interest as a potential alternative to fossil fuels (Pechsiri et al. 2016). The non-provisioning ecosystem services that can be provided by seaweeds (Rönnbäck et al. 2007) are also increasingly recognized and valued in the area. Support and stabilization of marine biodiversity, coastal protection and even an increased aesthetic value of cleaner and less degraded coastal environments are all services that can be provided to different degrees by the various types of natural seaweed ecosystems that exist in the area (Rönnbäck et al. 2007), as well as by the artificial habitats formed by seaweed aquaculture (Hasselstrom et al. 2018). However, conflicting interests to use coastal environments in other ways currently also emerge (e.g. Haller et al. 2011, Voss et al. 2017), which increases the necessity for a coastal management with a wider perspective.

Acknowledgments: The contribution of S.A.W. was supported by the Baltic Eye project.

References

- Almroth, E. and M.D. Skogen. 2010. A North Sea and Baltic Sea model ensemble eutrophication assessment. *Ambio* 39: 59–69.
- Alvarado-Morales, M., A. Boldrin, D.B. Karakashev, S.L. Holdt, I. Angelidaki and T. Astrup. 2013. Life cycle assessment of biofuel production from brown seaweed in Nordic conditions. *Bioresource Technol.* 129: 92–99.
- Arroyo, N.L., K. Aarnio, M. Mäensivu and E. Bonsdorff. 2012. Drifting filamentous algal mats disturb sediment fauna: Impacts on macro–meiofaunal interactions. *J. Exp. Mar. Biol. Ecol.* 420–421: 77–90.
- Bartsch, I. and R. Kühlenkamp. 2000. The marine macroalgae of Helgoland (North Sea): an annotated list of records between 1845 and 1999. *Helgoland Mar. Res.* 54: 160–189.
- Bartsch, I., C. Wiencke, K. Bischof, C.M. Buchholz, B.H. Buck, A. Eggert, P. Feuerpfeil, D. Hanelt, S. Jacobsen, R. Karez, U. Karsten, M. Molis, M.Y. Roleda, H. Schubert, R. Schumann, K. Valentin, F. Weinberger and J. Wiese. 2008. The genus *Laminaria* sensu lato: recent insights and developments. *Eur. J. Phycol.* 43: 1–86.
- Berglund, J., J. Mattila, O. Ronnberg, J. Heikkilä and E. Bonsdorff. 2003. Seasonal and inter-annual variation in occurrence and biomass of rooted macrophytes and drift algae in shallow bays. *Estuarine Coastal Shelf Sci.* 56: 1167–1175.
- Bergström, K. 2012. *Impact of using macroalgae from the Baltic Sea in biogas production: a review with special emphasis on heavy metals*. MSc-thesis, Linnæus University, Kalmar, Sweden. pp. 1–37.
- Blidberg, E. and F. Gröndahl. 2012. Macroalgae harvesting and cultivation. In: (A. Schultz-Zehden and M. Matczak, eds) *SUBMARINER compendium: an assessment of innovative and sustainable uses of baltic marine resources*. Maritime Institute, Gdansk. pp. 49–76.
- Bruhn, A., J. Dahl, H.B. Nielsen, L. Nikolaisen, M.B. Rasmussen, S. Markager, B. Olesen, C. Arias and P.D. Jensen. 2011. Bioenergy potential of *Ulva lactuca*: Biomass yield, methane production and combustion. *Bioresource Technol.* 102: 2595–2604.
- Bruhn, A., D.B. Tørring, M. Thomsen, P. Canal-Vergés, M.M. Nielsen, M.B. Rasmussen, K.L. Eybye, M.M. Larsen, T.J.S. Balsby and J.K. Petersen. 2016. Impact of environmental conditions on biomass yield, quality, and bio-mitigation capacity of *Saccharina latissima*. *Aquacult. Env. Interac.* 8: 619–636.
- Bučas, M., D. Daunys and S. Olenin. 2009. Recent distribution and stock assessment of the red alga *Furcellaria lumbricalis* on an exposed Baltic Sea coast: combined use of field survey and modelling methods. *Oceanologia* 51: 341–359.
- Bucholc, K., M. Szymczak-Żyła, L. Lubecki, A. Zamojska, P. Hapter, E. Tjernström and G. Kowalewska. 2014. Nutrient content in macrophyta collected from southern Baltic Sea beaches in relation to eutrophication and biogas production. *Sci. Tot. Env.* 473–474: 298–307.
- Buck, B.H. and C.M. Buchholz. 2004. The offshore-ring: a new system design for the open ocean aquaculture of macroalgae. *J. Appl. Phycol.* 16: 355–368.
- Buck, B.H. and B. Grote. 2019. Seaweed in high-energy environments: protocol to move *Saccharina* cultivation offshore. In: (B. Charrier, T. Wichard and C.R.K. Reddy, eds) *Protocols for macroalgae research*. CRC Press, Boca Raton. pp. 3–36.
- Bundesverband Aquakultur. 2019. Online available at: <https://www.bundesverband-aquakultur.de/Zuckertang>. In German. [Accessed 21 March 2019].
- Davidsson, Å. 2007. *Seaweed and algae as a natural resource and a renewable energy source, step 1*. Detox AB. pp. 1–28.
- Defeo, O., A. McLachlan, D.S. Schoeman, T.A. Schlacher, J. Dugan, A. Jones, M. Lastra and F. Scapini. 2009. Threats to sandy beach ecosystems: a review. *Estuar. Coast. Shelf Sci.* 81: 1–12.
- EEA. 2018. European waters – Assessment of status and pressures 2018. *European Environmental Agency Report 7/2018*: 1–90.
- Eriksson, B.K., G. Johansson and P. Snoeijs. 1998. Long-term changes in the sublittoral zonation of brown algae in the southern Bothnian Sea. *Eur. J. Phycol.* 33: 241–249.
- ESTAGAR. 2019. Online available at: <http://www.estagar.ee> [Accessed 21 June 2019].
- European Parliament and Council. 2014. Directive 2000/60/EC of 23 October 2000 establishing a framework for Community action in the field of water policy. Online available at: <http://data.europa.eu/eli/dir/2000/60/2014-11-20> [Accessed 07 September 2019].
- Ferdouse, F., S.L. Holdt, R. Smith, P. Murua and Z. Yang. 2018. *The global status of seaweed production, trade and utilization*. Food and Agriculture Organization of the United Nations, Rome, Italy. pp. 1–124.
- Filipkowska, A., L. Lubecki, M. Szymczak-Żyła, M. Łotocka and G. Kowalewska. 2009. Factors affecting the occurrence of algae on the Sopot beach (Baltic Sea). *Oceanologia* 51: 233–262.
- Franzén, D., E. Infantes and F. Gröndahl. 2019. Beach-cast as biofertiliser in the Baltic Sea region – potential limitations due to cadmium-content. *Ocean Coast. Manage.* 169: 20–26.
- Gilburn, A.S. 2012. Mechanical grooming and beach award status are associated with low strandline biodiversity in Scotland. *Estuar. Coast. Shelf Sci.* 107: 81–88.
- Grave, H. and H. Moeller. 1982. Quantification of dead marine plant biomass along the Baltic Sea coast of Western Germany. *Helgoländer Meeresuntersuchungen* 35: 517–519.
- Greger, M., T. Malm and L. Kautsky. 2007. Heavy metal transfer from composted macroalgae to crops. *Eur. J. Agronomy* 26: 257–265.
- Gröndahl, F. 2009. Removal of surface blooms of the Cyanobacteria *Nodularia spumigena*: a pilot project conducted in the Baltic Sea. *Ambio* 38: 79–84.
- Gustafsson, B.G., F. Schenk, T. Blenckner, K. Eilola, H.E. Meier, B. Muller-Karulis, T. Neumann, T. Ruoho-Airola, O.P. Savchuk and E. Zorita. 2012. Reconstructing the development of Baltic Sea eutrophication 1850–2006. *Ambio* 41: 534–548.
- Hafting, J.T., A.T. Critchley, M.L. Cornish, S.A. Hubley and A.F. Archibald. 2012. On-land cultivation of functional seaweed products for human usage. *J. Appl. Phycol.* 24: 385–392.
- Haglund, K. and M. Pedersén. 1988. Spray cultivation of seaweeds in recirculating brackish water. *Aquaculture* 72: 181–189.
- Haglund, K. and M. Pedersen. 1993. Outdoor pond cultivation of the subtropical marine red alga *Gracilaria tenuistipitata* in brackish water in Sweden. Growth, nutrient uptake, co-cultivation with rainbow trout and epiphyte control. *J. Appl. Phycol.* 5: 271–284.
- Haller, I., N. Stybel, S. Schuacher and M. Mossbauer. 2011. Will beaches be enough? *J. Coastal Res.* 61: 70–80.
- Hammann, M., B. Buchholz, R. Karez and F. Weinberger. 2013. Direct and indirect effects of *Gracilaria vermiculophylla* on native *Fucus vesiculosus*. *Aquat. Inv.* 8: 121–132.

- Hasselstrom, L., W. Visch, F. Grondahl, G.M. Nylund and H. Pavia. 2018. The impact of seaweed cultivation on ecosystem services – a case study from the west coast of Sweden. *Mar. Pollut. Bull.* 133: 53–64.
- HELCOM. 2012. Checklist of Baltic Sea macro-species. *Baltic Sea Environment Proceedings* 130: 1–203.
- Holdt, S.L. and M.D. Edwards. 2014. Cost-effective IMTA: a comparison of the production efficiencies of mussels and seaweed. *J. Appl. Phycol.* 26: 933–945.
- Holmer, M. and R.M. Nielsen. 2007. Effects of filamentous algal mats on sulfide invasion in eelgrass (*Zostera marina*). *J. Exp. Mar. Biol. Ecol.* 353: 245–252.
- Hou, X., J.H. Hansen and A.-B. Bjerre. 2015. Integrated bioethanol and protein production from brown seaweed *Laminaria digitata*. *Bioresource Technol.* 197: 310–317.
- Kaspersen, B.S., T.B. Christensen, A.M. Fredenslund, H.B. Møller, M.B. Butts, N.H. Jensen and T. Kjaer. 2016. Linking climate change mitigation and coastal eutrophication management through biogas technology: evidence from a new Danish bioenergy concept. *Sci. Tot. Env.* 541: 1124–1131.
- Kersen, P. 2013. *Red seaweeds Furcellaria lumbricalis and Coccotylus truncatus: community structure, dynamics and growth in the northern Baltic Sea*. PhD thesis, Tallinn University, Tallinn. pp. 127.
- Kersen, P. and G. Martin. 2007. Annual biomass loss of the loose-lying red algal community via macroalgal beach casts in the Vaeinameri area, NE Baltic Sea. *Proc. Estonian Acad. Sci. Biol. Ecol.* 56: 278–289.
- Kersen, P., H. Orav-Kotta, J. Kotta and H. Kuk. 2009. Effect of abiotic environment on the distribution of the attached and drifting red algae *Furcellaria lumbricalis* in the Estonian coastal sea. *Estonian J. Ecol.* 58: 245–258.
- Kersen, P., T. Paalme, L. Pajusalu and G. Martin. 2017. Biotechnological applications of the red alga *Furcellaria lumbricalis* and its cultivation potential in the Baltic Sea. *Bot. Mar.* 60: 207–218.
- Kireeva, M.S. 1961. Amount of *Furcellaria fastigiata* (Huds.) Lamour. in the Baltic Sea (Area of Saaremaa and Hiiumaa Islands) (in Russian). *Trudy NIIRH SNH Latv. SSR* 3: 411–417.
- Kireeva, M.S. 1965. Commercial resources of algae in the coastal seas of Soviet Union (in Russian). *Okeanologiya* 5: 14–21.
- Kostamo, K. 2008. *The life cycle and genetic structure of the red alga Furcellaria lumbricalis on a salinity gradient*. PhD-thesis, University of Helsinki, Helsinki, Finland.
- Kostamo, K., H. Korpelainen and S. Olsson. 2012. Comparative study on the population genetics of the red algae *Furcellaria lumbricalis* occupying different salinity conditions. *Mar. Biol.* 159: 561–571.
- Kotta, J., T. Paalme, P. Kersen, G. Martin, K. Herkuel and T. Moeller. 2008. Density dependent growth of the red algae *Furcellaria lumbricalis* and *Coccotylus truncatus* in the West Estonian Archipelago Sea, northern Baltic Sea. *Oceanologia* 50: 577–585.
- Kovtun, A., K. Torn and J. Kotta. 2009. Long-term changes in a northern Baltic macrophyte community. *Estonian J. Ecol.* 58: 270–285.
- Kruk-Dowgiatto, L. and A. Szaniawska. 2008. Gulf of Gdańsk and Buck Bay. In: (U. Schiewer, ed) *Ecology of Baltic Coastal waters*. Springer, Berlin. pp. 139–165.
- Lackschewitz, D., K. Reise, C. Buschbaum and R. Karez. 2014. *Neobiota in deutschen Küstengewässern*. Landesamt für Landwirtschaft, Umwelt und ländliche Räume des Landes Schleswig-Holstein (LLUR), Flintbek. pp. 216. (in German).
- Lauringson, V. and J. Kotta. 2006. Influence of the thin drift algal mats on the distribution of macrozoobenthos in Koiguste Bay, NE Baltic Sea. *Hydrobiologia* 554: 97–105.
- Lehmann, M.S.S. 1814. *Der entdeckte Nutzen des Seegrases zum Füllen der Küssen und Polster*. Sehnböthe, Kopenhagen/Danmark. pp. 23 (in German).
- Levring, T., H.A. Hoppe and O.J. Schmid. 1969. *Marine algae: a survey of research and utilization*. Cram, De Gruyter & Co, Hamburg. pp. 421.
- Lund, S. and J. Christensen. 1969. On the collection of *Furcellaria* in Denmark during the years. *Proc. Int. Seaweed Symp.* 6: 699–701.
- Lüning, K. and L. Mortensen. 2015. European aquaculture of sugar kelp (*Saccharina latissima*) for food industries: iodine content and epiphytic animals as major problems. *Bot. Mar.* 58: 449–455.
- Malm, T., S. Raberg, S. Fell and P. Carlsson. 2004. Effects of beach cast cleaning on beach quality, microbial food web, and littoral macrofaunal biodiversity. *Estuarine Coastal Shelf Sci.* 60: 339–347.
- Marinho, G., S. Holdt, M. J. Birkeland and I. Angelidaki. 2015a. Commercial cultivation and bioremediation potential of sugar kelp, *Saccharina latissima*, in Danish waters. *J. Appl. Phycol.* 27: 1963–1973.
- Marinho, G.S., S.L. Holdt, C. Jacobsen and I. Angelidaki. 2015b. Lipids and composition of fatty acids of *Saccharina latissima* cultivated year-round in integrated multi-trophic aquaculture. *Mar. Drugs* 13: 4357–4374.
- Martin, G., T. Paalme and H. Kuk. 1996. Long-term dynamics of the commercially usable *Furcellaria lumbricalis*-*Coccotylus truncatus* community in Kassari Bay, West Estonian Archipelago, the Baltic Sea. In: *Proceedings of Polish-Swedish symposium on Baltic Coastal fisheries, resources and management*. Sea Fisheries Institute, Gdynia (Poland). pp. 121–129.
- Martin, G., T. Paalme and K. Torn. 2006a. Growth and production rates of loose-lying and attached forms of the red algae *Furcellaria lumbricalis* and *Coccotylus truncatus* in Kassari Bay, the West Estonian Archipelago Sea. *Hydrobiologia* 554: 107–115.
- Martin, G., T. Paalme and K. Torn. 2006b. Seasonality pattern of biomass accumulation in a drifting *Furcellaria lumbricalis* community in the waters of the West Estonian Archipelago, Baltic Sea. *J. Appl. Phycol.* 18: 557–563.
- Martin, G., J. Kotta, T. Möller and K. Herkül. 2013. Spatial distribution of marine benthic habitats in the Estonian coastal sea, northeastern Baltic Sea. *Estonian J. Ecol.* 62: 165.
- Michalak, I., R. Wilk and K. Chojnacka. 2016. Bioconversion of Baltic seaweeds into organic compost. *Waste Biomass Valorization* 8: 1885–1895.
- Ministeriet for Fødevarer, Landbrug og Fiskeri. 2016. *Strategi for bæredygtig udvikling af akvakultursektoren i Danmark 2014–2020*. Copenhagen, Danmark. pp. 28. (in Danish).
- Møller Nielsen, M., C. Paulino, J. Neiva, D. Krause-Jensen, A. Bruhn and E.A. Serrão. 2016. Genetic diversity of *Saccharina latissima* (Phaeophyceae) along a salinity gradient in the North Sea–Baltic Sea transition zone. *J. Phycol.* 52: 523–531.

- Mossbauer, M., I. Haller, S. Dahlke and G. Schernewski. 2012. Management of stranded eelgrass and macroalgae along the German Baltic coastline. *Ocean Coast. Manage.* 57: 1–9.
- Nielsen, M.M., D. Manns, M. D'este, D. Krause-Jensen, M.B. Rasmussen, M.M. Larsen, M. Alvarado-Morales, I. Angelidaki and A. Bruhn. 2016. Variation in biochemical composition of *Saccharina latissima* and *Laminaria digitata* along an estuarine salinity gradient in inner Danish waters. *Algal Res.* 13: 235–245.
- Norkko, A. and E. Bonsdorff. 1996a. Altered benthic prey-availability due to episodic oxygen deficiency caused by drifting algal mats. *Mar. Ecol. Prog. Ser.* 17: 355–372.
- Norkko, A. and E. Bonsdorff. 1996b. Population responses of coastal zoobenthos to stress induced by drifting algal mats. *Mar. Ecol. Prog. Ser.* 140: 141–151.
- Nyberg, C.D., M.S. Thomsen and I. Wallentinus. 2009. Flora and fauna associated with the introduced red alga *Gracilaria vermiculophylla*. *Eur. J. Phycol.* 44: 395–403.
- Osterling, M. and L. Pihl. 2001. Effects of filamentous green algal mats on benthic macrofaunal functional feeding groups. *J. Exp. Mar. Biol. Ecol.* 263: 159–183.
- Paalme, T. 2017. *Estimations on the commercial red algal stock in Kassari Bay*. Project report LLTMI17261, University of Tartu, Estonia. (in Estonian).
- Paalme, T., G. Martin, J. Kotta, H. Kuk and K. Kaljurand. 2004. Distribution and dynamics of drifting macroalgal mats in Estonian coastal waters during 1995–2003. *Proc. Estonian Acad. Sci. Biol. Ecol.* 53: 260–268.
- Paalme, T., J. Kotta, P. Kersen, G. Martin, H. Kuk and K. Torn. 2011. Inter-annual variations in biomass of loose lying algae *Furcellaria–Coccolytus* community: the relative importance of local versus regional environmental factors in the West Estonian Archipelago. *Aquat. Bot.* 95: 146–152.
- Paalme, T., J. Kotta and P. Kersen. 2013. Does the growth rate of drifting *Furcellaria lumbricalis* and *Coccolytus truncatus* depend on their proportion and density? *Proc. Estonian Acad. Sci. Biol. Ecol.* 62: 141–147.
- Pärt, S. 2013. *Spatial variability of loose-lying red algal community in the Kassari Bay*. MSc thesis, University of Tartu, Estonia.
- Pechsiri, J.S., J.E. Thomas, E. Risen, M.S. Ribeiro, M.E. Malmstrom, G.M. Nylund, A. Jansson, U. Welander, H. Pavia and F. Grondahl. 2016. Energy performance and greenhouse gas emissions of kelp cultivation for biogas and fertilizer recovery in Sweden. *Sci. Total Environ.* 573: 347–355.
- Pedersen, M. and P. Snoeijs. 2001. Patterns of macroalgal diversity, community composition and long-term changes along the Swedish west coast. *Hydrobiologia* 459: 83–102.
- Quillien, N., M.C. Nordstrom, G. Schaal, E. Bonsdorff and J. Grall. 2016. Opportunistic basal resource simplifies food web structure and functioning of a highly dynamic marine environment. *J. Exp. Mar. Biol. Ecol.* 477: 92–102.
- Remane, A. 1934. Die Brackwasserfauna. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 36: 34–74. (in German).
- Riemann, B., J. Carstensen, K. Dahl, H. Fossing, J.W. Hansen, H.H. Jakobsen, A.B. Josefson, D. Krause-Jensen, S. Markager, P.A. Stæhr, K. Timmermann, J. Windolf and J.H. Andersen. 2015. Recovery of Danish coastal ecosystems after reductions in nutrient loading: a holistic ecosystem approach. *Estuaries Coasts* 39: 82–97.
- Risén, E. 2014. *Sustainability aspects of bioenergy and nutrient recovery from marine biomass – Baltic Sea case studies*. PhD thesis, KTH – Royal Institute of Technology, Stockholm, Sweden. pp. 57.
- Risén, E., O. Tatarchenko, F. Gröndahl and M.E. Malmström. 2014. Harvesting of drifting filamentous macroalgae in the Baltic Sea: an energy assessment. *J. Renewable. Sustainable Energy* 6: 013116.
- Risén, E., J. Nordström, M.E. Malmström and F. Gröndahl. 2017. Non-market values of algae beach-cast management – Study site Trelleborg, Sweden. *Ocean Coast. Manage.* 140: 59–67.
- Rohde, S., C. Hiebenthal, M. Wahl, R. Karez and K. Bischof. 2008. Decreased depth distribution of *Fucus vesiculosus* (Phaeophyceae) in the Western Baltic: effects of light deficiency and epibionts on growth and photosynthesis. *Eur. J. Phycol.* 43: 143–150.
- Rönnbäck, P., N. Kautsky, L. Pihl, M. Troell, T. Soerqvist and H. Wennhage. 2007. Ecosystem goods and services from Swedish coastal habitats: identification, valuation, and implications of ecosystem shifts. *Ambio* 36: 534–544.
- Ronnberg, C. and E. Bonsdorff. 2004. Baltic Sea eutrophication: area-specific ecological consequences. *Hydrobiologia* 514: 227–241.
- Russell, G. 1988. The seaweed flora of a young semi-enclosed sea: the Baltic. Salinity as a possible agent of flora divergence. *Helgoländer Meeresuntersuchungen* 42: 243–250.
- Salovius, S., M. Nyqvist and E. Bonsdorff. 2005. Life in the fast lane: macrobenthos use temporary drifting algal habitats. *J. Sea Res.* 53: 169–180.
- Sandow, V. 2007. Kurzbeitrag: Polykultur in der Ostsee – Vision und Realisierung. *Rostocker Meeresbiologische Beiträge* 17: 125–127. (in German).
- Schories, D., C. Pehlke and U. Selig. 2009a. Depth distributions of *Fucus vesiculosus* L. and *Zostera marina* L. as classification parameters for implementing the European Water Framework Directive on the German Baltic coast. *Ecol. Indicators* 9: 670–680.
- Schories, D., U. Selig and H. Schubert. 2009b. Species and synonym list of the German marine macroalgae based on historical and recent records. *Rostocker Meeresbiologische Beiträge* 21: 7–135.
- Schramm, W. 1996. The Baltic Sea and its transition zones. In: (W. Schramm and P. Nienhuis, eds) *Marine benthic vegetation – recent changes and the effects of eutrophication*. Springer-Verlag, Berlin, Germany. pp. 131–164.
- Schramm, W. 1998. Seaweed resources of the Baltic Sea and the German coasts of the North Sea. In: (A.T. Critchley and H. Ohno, eds) *Seaweed resources of the World*. Japan International Collaboration Agency. pp. 226–232.
- Schubert, H., P. Feuerpfeil, R. Marquardt, I. Telesh and S. Skarlato. 2011. Macroalgal diversity along the Baltic Sea salinity gradient challenges Remane's species-minimum concept. *Mar. Pollution Bull.* 62: 1948–1956.
- Seghetta, M., D. Tørring, A. Bruhn and M. Thomsen. 2016. Bioextraction potential of seaweed in Denmark – An instrument for circular nutrient management. *Sci. Tot. Environ.* 563–564: 513–529.
- Snoeijs, P. 1999. Marine and brackish waters. *Acta Phytogeographica Suecica* 84: 187–212.
- Steinhagen-Schneider, G. 1981. *Fucus vesiculosus* als Schwermetall-Bioakkumulator. *Der Einfluss von Temperatur, Salzgehalt, und Metallkombination auf die Inkorporationsleistung*. PhD-thesis, Christian-Albrechts-Universität Kiel, Germany. pp. 53 (in German).

- Steinhagen, S., F. Weinberger and R. Karez. 2018. Molecular analysis of *Ulva compressa* (Chlorophyta, Ulvales) reveals its morphological plasticity, distribution and potential invasiveness on German North Sea and Baltic Sea coasts. *Eur. J. Phycol.* 54: 102–114.
- Suutari, M., E. Leskinen, K. Spilling, K. Kostamo and J. Seppälä. 2017. Nutrient removal by biomass accumulation on artificial substrata in the northern Baltic Sea. *J. Appl. Phycol.* 29: 1707–1720.
- Torn, K., D. Krause-Jensen and G. Martin. 2006. Present and past depth distribution of bladderwrack (*Fucus vesiculosus*) in the Baltic Sea. *Aquat. Bot.* 84: 53–62.
- Trei, T. 1978. The physiognomy and structure of the sublittoral macrophyte communities in Kassary Bay (an area between the Isles of Hiiumaa and Saaremaa). *Kieler Meeresforschungen* 4: 117–121.
- Tuvikene, R. and M. Robal. 2015a. *Isolation of the polysaccharides from the red algae Furcellaria lumbricalis and Coccotylus truncatus*. Project report TP/8014, Tallinn University. (in Estonian)
- Tuvikene, R. and M. Robal. 2015b. *Proteinic pigments from the red alga Furcellaria lumbricalis: content and isolation possibilities*. Project report TP/9314, Tallinn University. (in Estonian)
- Tuvikene, R., K. Truus, M. Vaher, T. Kailas, G. Martin and P. Kersen. 2006. Extraction and quantification of hybrid carrageenans from the biomass of the red algae *Furcellaria lumbricalis* and *Coccotylus truncatus*. *Proc. Estonian Acad. Sci. Chem.* 55: 40–53.
- Tuvikene, R., K. Truus, M. Robal, O. Volobujeva, E. Mellikov, T. Pehk, A. Kollist, T. Kailas and M. Vaher. 2010. The extraction, structure, and gelling properties of hybrid galactan from the red alga *Furcellaria lumbricalis* (Baltic Sea, Estonia). *J. Appl. Phycol.* 22: 51–63.
- Vaheri, P., A. Mäkinen, S. Salovius and S. Vuorinen. 2000. Are drifting algal mats conquering the bottom of the Archipelago Sea, SW Finland? *Ambio* 29: 338–343.
- Vanhooren, S., H. Maelfait and K. Belpaeme. 2011. Moving towards an ecological management of the beaches. *J. Coastal Res. SI61*: 81–86.
- Veide Vilg, J., G.M. Nylund, T. Werner, L. Qvirist, J.J. Mayers, H. Pavia, I. Undeland and E. Albers. 2015. Seasonal and spatial variation in biochemical composition of *Saccharina latissima* during a potential harvesting season for Western Sweden. *Bot. Mar.* 58: 435–447.
- Vollbrecht, K. 1973. Der Küstenrückgang an der Insel Sylt. *Deutsche Hydrografische Zeitschrift* 26: 155–170 (in German).
- Voss, R., M.F. Quaas, J. Hoffmann and J.O. Schmidt. 2017. Chapter 17 – Social-ecological tradeoffs in Baltic Sea fisheries management. In: (P.S. Levin and M.R. Poe, eds) *Conservation for the anthropocene ocean*. Academic Press. pp. 359–377.
- Wang, G., L. Chang, R. Zhang, S. Wang, X. Wei, E. Rickert, P. Krost, L. Xiao and F. Weinberger. 2019. Can targeted defense elicitation improve seaweed aquaculture? *J. Appl. Phycol.* 31: 1845–1854.
- Weinberger, F., M. Hammann, M. Griem and D. Siedentopp. 2013. *Ostsee-Makroalgenblüten. Forschungsbericht zur Einschätzung der möglichen künftigen Ausbildung von Makroalgenblüten an*

der deutschen Ostseeküste. Project report, GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel. pp. 143 (in German).

Bionotes



Florian Weinberger

GEOMAR Helmholtz-Institute for Ocean Science, Marine Ecology Division, D-24105 Kiel, Germany. <https://orcid.org/0000-0003-3366-6880>
fweinberger@geomar.de

Florian Weinberger is a senior scientist at the GEOMAR Helmholtz Centre for Ocean Research at Kiel in Germany. His research focus is on the ecology of nuisance seaweeds, on the eco-evolutionary implications of seaweed invasions and on the microbiological and molecular biological aspects of seaweed and aquatic plant ecology.



Tiina Paalme

Estonian Marine Institute, University of Tartu, Tartu, Estonia

Tiina Paalme is a senior scientist at the Estonian Marine Institute, University of Tartu (Estonia). Her research focus is on the ecophysiology of brackish water macrophytes, including the estimation of the effects of climatic, environmental and anthropogenic factors on primary production and growth of different macroalgal species in the Baltic Sea.



Sofia A. Wikström

Baltic Sea Centre, Stockholm University, SE-106 91 Stockholm, Sweden

Sofia A. Wikström is an associated professor in marine ecology at Stockholm University (Sweden). Her main research field is ecology of benthic macrophytes in the Baltic Sea, including ecological functions of benthic vegetation and the response of coastal habitats to anthropogenic disturbance.